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Ecological and Evolutionary Determinants of the Species-Area Relation in Caribbean Anoline Lizards

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Ecological and evolutionary determinants of the species–area relation in Caribbean anoline lizards

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SUMMARY

Species–area relations were studied for anoline lizards on 147 islands in the Caribbean. The relative importance of ecological and evolutionary factors in determining species number varied with island size. On small islands, only ecological factors affect the species–area relation. Further, the importance of different ecological factors such as colonization, competition, and extinction, varied among different types of islands. On landbridge islands, differential extinction as a function of island area appears to play a key role in producing a species–area relation. By contrast, limited colonization success generally prevents ocean islands from accumulating more than two species. Among the larger islands, evolutionary factors are the primary determinant of species number. Detailed examination of several components of evolutionary diversification indicates that the species–area relation among the Greater Antilles primarily results because larger islands have increased number of habitat niches occupied and a greater number of closely related species that are ecologically similar and allopatrically distributed; increased subdivision of certain habitats plays a lesser role.

1. INTRODUCTION

Explaining differences in species diversity among areas has been a central goal of ecology with studies traditionally focusing either on historical or ecological factors (see recent reviews in Ricklefs & Schluter 1993; Brown 1995; Rosenzweig 1995). Studies of insular faunas and floras have played a prominent role in the development of theories of species diversity beginning with the work of the naturalists of the latter half of the 19th century and continuing to this day. MacArthur & Wilson's (1967) equilibrium theory of island biogeography, which explained differences in diversity in terms of the ecological processes of colonization and extinction, was particularly influential. Nonetheless, as MacArthur & Wilson (1967, chapter 7) noted, ecological factors are only part of the explanation. To the extent that *in situ* evolutionary diversification contributes to the species diversity of an island, then evolutionary, as well as ecological, factors must be considered. To date, however, few studies have attempted to consider the relative roles of ecological and evolutionary factors in determining species diversity. One possible explanation for the paucity of such studies is that few groups of organisms occur in a wide enough range of situations that the role of both ecological and evolutionary factors can be examined. Caribbean *Anolis* lizards, however, are an exception to this generality.

Anolis lizards are arguably the dominant group of vertebrates in the Caribbean (their only rival being frogs of the genus *Eleutherodactylus*). Anoles are found on almost every island throughout the Caribbean (Williams 1969), often at extremely high densities (Schoener & Schoener 1980; Reagan 1992). One hundred and thirty eight species are currently recognized, with as many as 54 on a single island (Powell *et al.* 1996). The distribution of anole lineages among islands in the Caribbean paradoxically suggests both great dispersal ability and relatively limited dispersal success. The former is demonstrated by the presence of some Cuban species of anoles on islands 250 or more miles from Cuba (e.g. Swan Island, Bay Islands; see Williams 1969). These islands are relatively low-lying and must have been underwater during the last glacial minimum, 120000 years ago. Hence, colonization of these distant islands has occurred relatively recently.

Despite this great colonizing capability, however, anole faunas throughout the Caribbean are not homogeneous; rather, the vast majority (> 85 %) of species of *Anolis* are endemic to a single island bank (this number is only slightly inflated by the tendency to describe closely related taxa on different islands as different species). This paradox indicates that both ecological and evolutionary factors must be considered in studies of the island biogeography of Caribbean anoles. In addition, many island banks emergent 8000 years ago have been fragmented by rising sea-levels (figure 1); thus, historical factors, too, must be considered to understand patterns of anole species-distribution.

2. DATABASE

The primary source of data for this paper is Rand's (1969) compilation of area and species number for 145 Caribbean islands ranging in area from 0.06 → > 40000 mi². I have updated the species counts following Powell *et al.* (1996) for the Greater Antilles and Schwartz & Henderson (1991) for islands near His-

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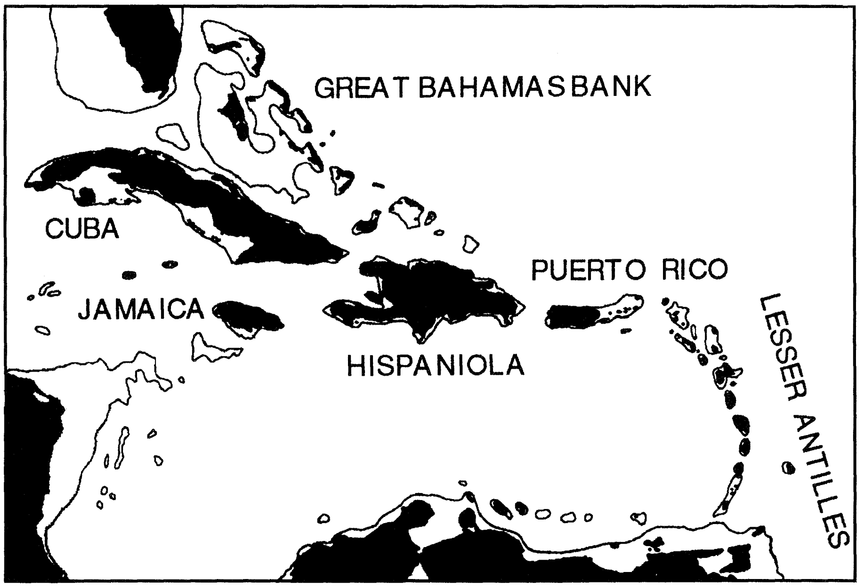

Figure 1. Map of the Caribbean. Lines represent 200 m depth contours. At times of lower sea-levels, these island banks were above water, thus merging currently independent islands into single large landmasses.

paniola and the Isle of Pines. In addition, I have added data for two additional Hispaniolan islands, Beata and Ilé a Cabrit (Schwartz & Henderson 1991).

Rand (1969) classified the islands into four groups: Greater Antilles and fringing islands, Lesser Antilles, isolated islands (i.e. islands in the vicinity of the Greater Antilles, such as St. Croix and Mona, that have never been part of a larger island), and the Bahamas. For reasons discussed below, I separate the four large Greater Antillean islands from islands on the same underwater banks; the former I refer to as the ‘Greater Antilles’ and the latter as ‘Greater Antillean satellites’. In addition, I divide the Bahamian islands into those on the Great Bahama Bank and those on other banks; although the latter constitutes a heterogeneous group, all members of this group are similar in being isolated and occurring on relatively small island banks.

3. SPECIES–AREA RELATIONS IN *ANOLIS*

A significant relation exists between island area and species number for Caribbean *Anolis* (figure 2). MacArthur & Wilson (1967) noted that the species–area relation could be described by the equation $s = ca^z$, where s is the number of species, a is island area, and c and z are constants. MacArthur & Wilson further noted that the value of z normally lies in the range 0.20–0.35; subsequent work showed that many types of organisms have z-values in this range (Connor & McCoy 1979). For Caribbean *Anolis*, $z = 0.13$ (as calculated from log-log regressions), a value lower than that observed for most other taxa.

Separate analyses, however, indicate substantial heterogeneity in the species–area relation among island classes (figures 2 and 3). No relation exists for isolated ($r^2 = 0.00$, $F_{1,9} = 0.18$, $P > 0.65$) and ‘other’ (= non-Great Bahama Bank) Bahamian islands ($r^2 = 0.01$, $F_{1,36} = 1.36$, $P > 0.25$) and only a weak relation exists for Lesser Antillean islands ($r^2 = 0.13$, $F_{1,31} = 5.89$, $P < 0.025$). By contrast, area and species number are strongly related for Greater Antillean ($r^2 = 0.92$, $F_{1,2} = 36.75$, $P < 0.03$), Greater Antillean satellite ($r^2 = 0.54$, $F_{1,44} = 53.60$, $P < 0.001$), and Great Bahamas Bank islands ($r^2 = 0.67$, $F_{1,13} = 29.30$, $P < 0.001$). Among these latter three classes, the slope of the regression lines differs between the Greater Antilles and the other two (ANCOVA [analysis of covariance]: Greater Antilles ($z = 0.77$) versus satellites ($z = 0.18$), $F_{1,46} = 10.75$, $P < 0.0025$; Greater Antilles versus Great Bahamas ($z = 0.19$), $F_{1,15} = 11.41$, $P < 0.005$); the regression lines for the Greater Antillean satellite and Great Bahamas Bank islands also are almost statistically different in intercept ($F_{1,58} = 3.46$, $P < 0.07$).

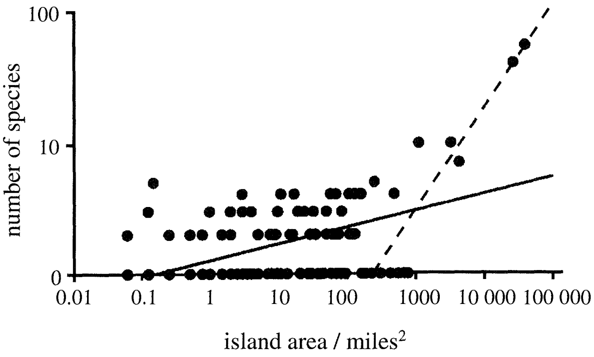

Figure 2. Species–area relation for Caribbean *Anolis*. The solid line is the best fit least squares regression line for all islands; the hatched line is the line for only the major islands of the Greater Antilles (Cuba, Hispaniola, Jamaica and Puerto Rico).

Rand (1969) previously noted this heterogeneity among island classes. He further noted that among islands that are not on the island banks of the Greater Antilles or on the Great Bahamas Bank, not only is the relation between island area and number of species weak or non-existent, but no island has more than two species. By contrast, Greater Antillean satellites can

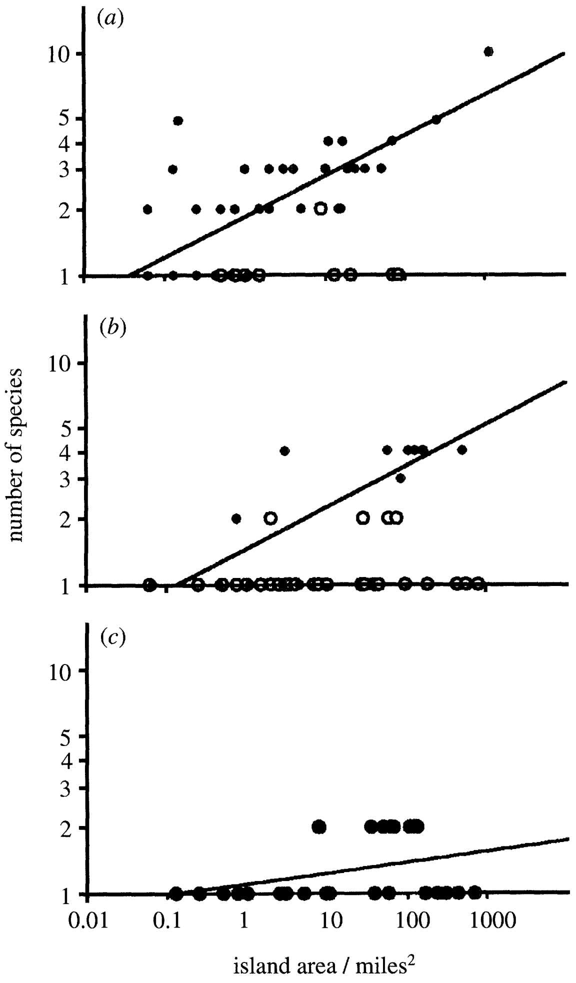

Figure 3. Species–area relation for several classes of islands. (*a*) Greater Antillean Satellite islands; closed circles are islands on the banks of the Greater Antilles, whereas open circles are isolated islands (i.e. islands that have never been connected by dry land to one of the Greaer Antilles). The Greater Antilles (Jamaica, Puerto Rico, Hispaniola, and Cuba) are not included in this graph. (*b*) Bahamian islands; closed circles are islands of the Great Bahama Bank and open circles are other islands. (*c*) Lesser Antillean islands. For all graphs, regression lines are only provided for statistically significant relations.

have as many as ten species and Great Bahamian Bank islands as many as four. One possible explanation for this difference is that isolated islands are more distant from sources of colonists than are satellite islands. To test this hypothesis, I measured the distance of each island to the nearest landmass with many potential colonizing species (Cuba, Hispaniola, Jamaica, Puerto Rico, or South America). Based on these measurements, a weak negative relation exists between species number and distance ($r^2 = 0.055$, $F_{1,91} = 6.32$, $P < 0.02$; sample sizes are smaller in this analysis than previous ones because some of the small islands reported by Rand (1969) could not be located); with the effect of island area removed by calculating residuals, relative species number is more strongly related to relative distance ($r^2 = 0.122$, $F_{1,91} = 13.73$, $P < 0.001$). Nonetheless, distance effects do not account for the difference in species number between landbridge (i.e. Greater Antillean and Great Bahama Bank) and isolated islands. With the effect of distance removed using residuals, the relation between area and species number is stronger for landbridge islands (i.e. islands formerly part of larger land masses) than it is for isolated islands both in the Greater Antilles (ANCOVA, difference in slopes, $F_{1,33} = 4.52$, $P < 0.05$) and in the Bahamas (difference in slopes, $F_{1,27} = 11.30$, $P < 0.0025$).

The difference in number of species on isolated versus landbridge islands obviously results from how the species came to be on the islands. Islands that were connected to larger landmasses can 'inherit' great numbers of species, whereas isolated islands that must build up species diversity via overwater colonization can manage two species at best (Rand 1969). The discrepancy suggests that, although *Anolis* has great dispersal capabilities, colonists arriving on inhabited islands must have very low likelihood of becoming established and that this likelihood diminishes as a function of number of species already resident on an island (Rand 1969). Further, all two-species isolated islands contain species that differ ecologically (Schoener 1970, 1988). With one possible exception (the northern Lesser Antilles, where character displacement may have produced ecological differentiation subsequent to sympatry [Schoener 1970; Losos 1990*b*; Miles & Dunham 1996; Schneider *et al.* 1996]), the differences between species on two-species islands existed before sympatry; in other words, a colonizing species must be ecologically different from a resident species if it is to have any substantial hope of successful colonization.

The Great Bahamas Bank is an exception to the generalization that no more than two species can colonize an island by overwater dispersal. None of the four species found on the Great Bahamas Bank evolved there; three immigrated from Cuba and one from Hispaniola. As with other isolated islands, the species that colonized the Great Bahamas Bank are all ecologically distinctive and each had evolved specializations to use a different habitat type before colonization of the Great Bahamas Bank (Schoener 1968). The greater number of colonists on the Great Bahamas bank relative to other isolated islands may be a reflection of lack of isolation; at its maximal exposure, this bank was only 10 miles from Cuba. The size of the Great Bahamas Bank may also have been important; at its maximal extent, it rivalled Cuba in total area.

The Greater Antilles themselves have also been colonized, although a precise estimate of the number of successful colonization events cannot be determined until phylogenetic relations of *Anolis* are better understood (see below). Nonetheless, the occurrence of colonization on these large islands indicates that a relation exists between area and the number of species that can successfully colonize an island (Williams 1969).

4. THE ROLE OF EXTINCTION

On the satellite islands of the Greater Antilles and within the Greater Bahamas Bank, extinction, rather than colonization, has been the primary process producing species–area patterns (Rand 1969). These islands fit the classic idea of faunal relaxation (Wilcox 1978; Richman *et al.* 1988), in which areas that presumably used to harbour more species experience decline in species richness after a reduction in island size. Such patterns have usually been explained as differential extinction, an explanation that seems to hold for Caribbean anoles. Previous studies on Bahamian (Schoener & Schoener 1983*a*, *b*) and Puerto Rican (Mayer 1989; Roughgarden 1989) islands indicate that species extinction is not random; rather, species drop out in a pattern predictable based on island area, thus producing a nested pattern of species occurrences.

The cause of this nesting of species probably is a result of habitat specializations. Islands lose habitats in a predictable pattern as they get smaller, which would result in a deterministic pattern of species disappearance. For example, in the Bahamas, the smallest lizard-inhabited islands are scrubby, with little vegetation. Such habitat is only suitable for *A. sagrei*. Larger islands may have thicker vegetation and some trees, providing habitat for *A. carolinensis smaragdinus*. Even larger islands will have the broad diameter trees and shade needed by *A. distichus*. Only the largest islands have the high vegetation necessary for the twig anole, *A. angusticeps* (Schoener & Schoener 1983*a*).

Colonization may play a secondary role in determining species occurrences on these islands by re-establishing or maintaining populations threatened by extinction (i.e. the 'rescue effect'; see Brown & Kodric-Brown 1977). For example, in the Bahamas, distance to a large source island is negatively related to species occurrences, although the relation is considerably weaker than that between species' occurrences and island area (Schoener & Schoener 1983*a*, *b*). This distance effect could result either because colonization occurs more frequently on less isolated islands or because more isolated islands have less suitable habitats, even when the effect of area is removed (Schoener & Schoener 1983*b*).

5. THE ROLE OF EVOLUTIONARY DIVERSIFICATION

Thus far, discussion has focused on ecological processes – colonization, competition, extinction – and how they are affected by island area. However, this discussion does not pertain to the large islands of the Greater Antilles, for the great bulk of their species has arisen *in situ* as a result of within-island speciation (Williams 1983). Thus, the processes responsible for the species–area curve among these islands must be fundamentally different from those operating within the smaller islands of the Caribbean.

First, one must ask if there is an island size below which within-island diversification does not occur. Williams (1983; also Williamson 1981) argued that cladogenetic speciation in anoles occurs only on islands the size of Puerto Rico or larger. This hypothesis may be tested by considering the phylogenetic relations of anoles. Within-island speciation would be suggested if sister taxa occur on the same island (or islands); between-island speciation would be suggested if the sister taxa occur on different islands (Lynch 1989; Brooks & McLennan 1991). This approach is not infallible; dispersal and shifts in geographic range can obscure these patterns (Losos & Larson, unpublished). Nonetheless, in this case the method seems reasonable because dispersal and range shifts are more likely to pose problems in a continental setting than in an island situation in which dispersal appears limited. Thus, dispersal and range shifts probably do not confound interpretation of general patterns of anole diversification, although they may be important in particular situations.

Within-island speciation clearly has occurred in the Greater Antilles. Of the 18 monophyletic groups (i.e. 'series') of anoles that occur in the Greater Antilles (Burnell & Hedges 1990; Hass *et al.* 1993), only four have species that occur on more than one island group. Hence, all of the diversification in the other 14 groups must have resulted from within-island speciation, rather than colonization from other islands. Even in the four species groups with species on different island groups, most of the speciation was probably within-island with one or two instances of between island speciation. Thus in the Greater Antilles, most speciation must have occurred by within-island diversification.

By contrast, on islands other than the Greater Antilles, only two instances exist of sister taxa occurring on the same island or group of islands, and neither provides a compelling case for within-island speciation. In the northern Lesser Antilles, the *wattsi* and *bimaculatus* groups are sister taxa. Members of the *wattsi* group only occur on six islands (and surrounding cays), all of which are occupied by members of the *bimaculatus* group (Schoener 1970; Lazell 1972). Thus, this pattern of geographic distribution is consistent with the hypothesis that the two lineages initially diverged on one of these islands; however, a more likely explanation, also consistent with the biogeographical data, is that the lineages diverged on different islands in the area and then subsequently came into sympatry. Similarly, *A. pigmaequestris* appears to be sympatric throughout its limited range in the northern Cuban fringing islands with its sister taxon, *A. equestris* (Garrido 1975). As with the case above, allopatric speciation followed by dispersal seems more likely than within-island diversification on these small islands.

Although mechanisms of speciation have been little explored in *Anolis*, the finding of a minimum island area below which within-island speciation probably does not occur is consistent with a hypothesis that geographic isolation is required for speciation. Small islands may not have the landscape necessary to produce geographic disjunction. Certainly, the landscape complexity of the Greater Antilles exceeds that of smaller Caribbean islands; in addition, the Greater Antilles have considerably more offshore islands upon which peripatric speciation might produce new species able to subsequently reinvade the larger island (Williams 1983). This explanation, however, is not entirely satisfying because some of the larger Lesser Antillean islands (e.g. Guadeloupe) are topographically diverse and have offshore islands, yet speciation has not occurred and these islands have no more than two species (note, too, that some of these islands appear as vegetationally complex as the Greater Antilles and certainly have the habitat complexity to support more than two species). More detailed studies of geographic differentiation and speciation in *Anolis* are required to more adequately address these issues.

Given that within-island speciation has been the predominant factor in the Greater Antilles, one might inquire what role colonization has played in establishing the species–area relation within these islands. As mentioned above, a more precise estimate of the role of colonization cannot be derived until phylogenetic relations among anoles are better understood. Nonetheless, a maximal estimate for the number of possible colonization events can be derived by counting the number of monophyletic species groups on each island (from Burnell & Hedges 1990; Hass *et al.* 1993), with the assumption that each species group represents a separate colonization event. Numbers obtained in this way will surely overstate the amount of colonization because two monophyletic groups on an island may be sister-taxa and thus not represent separate invasions and because the presence of some lineages may result from vicariance rather than dispersal (see discussion in Hedges 1992; Crother & Guyer 1996). Given these caveats, the maximal number of colonization events for each island are: Jamaica, 2 (29% of species on the island); Puerto Rico, 3 (30%); Hispaniola, 11 (28%); Cuba, 7 (13%). Thus, minimally, at least 70% of species on each of the Greater Antillean islands has arisen from *in situ* speciation.

6. CAUSES OF THE RELATION BETWEEN ISLAND AREA AND SPECIATION

The observed increase in species number with area in the Greater Antilles is a composite of several different factors, each of which may be affected differently by increasing island area. At the broadest level, two factors appear responsible for the increase in species number with area (Williams 1983). First, on larger islands, some species groups have produced a large number of geographically isolated species. For example, the *sagrei* species series has produced 14 ecologically similar species on Cuba, only two of which are distributed island-wide and most of which have relatively small geographic ranges. A similar pattern exists among the 14 grass anoles in the *alutaceus* series in Cuba. By contrast, most species in Jamaica and Puerto Rico are geographically widespread; only one species in Jamaica and two in Puerto Rico have geographically limited ranges. Second, the maximum number of anole species that can be found sympatrically increases with island area, from six in Jamaica to 12 on Cuba (figure 4). This increase in sympatric species is accomplished by both more finely subdividing the habitat and by utilizing additional niches.

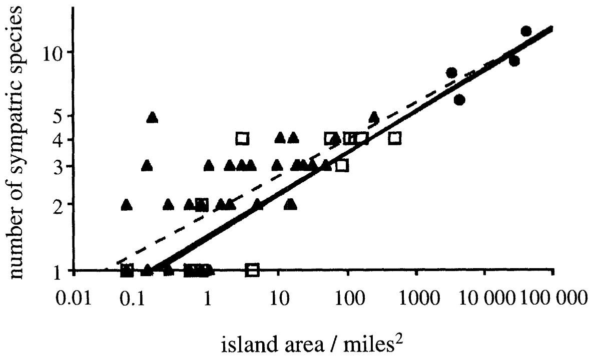

Figure 4. Maximum number of sympatric species vs. island area; closed circles are Greater Antilles, closed triangles are Greater Antillean satellite islands, open squares are Great Bahamas Bank. The relation is weak or nonexistent for islands of the Lesser Antilles, isolated islands in the Greater Antilles, and non-Great Bahama Bank Bahamian islands; hence, they are not included. The dashed line is the regression for the Greater Antilles; the solid lines are for Great Bahamas Bank and satellite islands.

To quantify these factors, I classified Greater Antillean *Anolis* species diversity into four categories. First, I counted the number of independent habitat niches that have been occupied on each island. On Puerto Rico, for example, species adapted to five niches have evolved: trunk-ground, trunk-crown, grass, crown-giant, and twig anoles (Williams 1972). Morphology was used as an index of habitat specialization. As a general rule, this assumption is not problematic; among all *Anolis* lizards that have been well-studied, morphologically different species differ in habitat use (e.g. Moermond 1979; Estrada & Silva Rodríguez 1984; Losos 1990*a*; Irschick & Losos 1996). Consequently, I counted the number of morphologically distinctive species on an island. For example, the 14 grass anoles of the *alutaceus* species group on Cuba were counted as one instance of habitat specialization.

Evolutionarily independent occupation by two lineages of the same habitat niche on the same island was counted as two events; however, this rarely occurred. The only examples are the multiple evolution of grass anoles on Cuba and Hispaniola and of twig anoles on Hispaniola. In addition, two lineages of trunk-ground anoles are present in Jamaica, but one, *A. sagrei*, is a recent colonist (Williams 1969).

Within each habitat niche, I investigated how many species have evolved the capability to be sympatric. For example, among the *alutaceus* series, as many as three species may be found sympatrically (Garrido & Hedges 1992). Hence, for this group, I scored one evolution of habitat niche specialization (grass anole) and two instances of the evolution of the ability to occur sympatrically. I broke down this latter category into two groupings, thermal differentiation and other. Coexistence of anoles using the same structural habitat by adapting to different thermal microclimates has been extensively documented in anoles as one means of permitting sympatry (reviewed in Losos 1994). Other means of attaining sympatry includes divergence in body size, which has occurred several times (e.g. *grahami* and *opalinus* on Jamaica, *evermanni* and *stratulus* on Puerto Rico; reviewed in Losos 1994). The ecology of a number of sympatric species, such as Cuban grass anoles, has not been well-studied. Hence, whether these species differ ecologically cannot at this time be

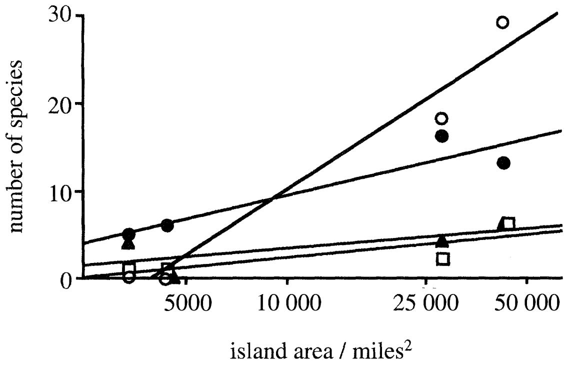

Figure 5. Species–area relation for several aspects of evolutionary diversification in the Greater Antilles. The species on each island are divided into four categories. Habitat (closed circles) refers to the number of different habitats occupied on an island. In the few instances in which two species (or clades) have adapted to use the same habitat on an island, both taxa are counted in the habitat category. When members of a monophyletic group use the same habitat, then the species are divided into three categories: allospecies (open circles) refers to allopatrically distributed species, thermal (closed triangles) refers to sympatric species that use different thermal microhabitats, and sympatric (open squares) includes all other sympatric species. See text for more details. Islands are (from left to right) Puerto Rico, Jamaica, Hispaniola and Cuba.

assessed; based on studies of other sympatric anoles, I would suspect that ecological differences will be found upon closer examination; in any case, they are placed in the 'other' category.

Finally, I categorized all remaining taxa (e.g. the remaining 11 members of the *alutaceus* series) as allopatric species; i.e. members of a species complex that are ecologically undifferentiated and allopatrically or parapatrically distributed. A potential bias exists in this procedure. First, in the absence of more detailed phylogenetic information, I assumed that the capability to achieve sympatry had evolved the minimum number of times consistent with the data. For example, many members of the *alutaceus* series occur sympatrically with one or two other members of that series, although no more than three species occur at any one site. The possibility exists that each one of these species has independently evolved the capability of coexisting with other members of its series. However, the alternative possibility is that the ability to exist sympatrically only evolved in three lineages within the *alutaceus* series, and that these lineages then produced a number of allopatrically distributed trios of species. Obviously, further phylogenetic information is needed to clarify this issue; the possibility exists that my method inflates the importance of allopatric diversification and diminishes the importance of ecological differentiation permitting coexistence among species adapted to the same habitat niche.

Given this categorization, figure 5 yields several insights. First, almost all species in Jamaica and Puerto Rico differ in habitat use, but allopatric species are the largest component of the Cuban fauna and a major component in Hispaniola. Second, the increase in species number with area primarily results from increases in number of habitat niches utilized and in the number of ecologically similar but allopatrically distributed species; the slope of increase for number of allopatric species is substantially greater than for habitat types (ANCOVA, $F_{1,4} = 13.59$, $P < 0.025$). Third, the number of species that coexist by using different thermal microclimates is approximately equal on three of the islands, but anomalously low for Jamaica.

Another point, not evident from the figure, is that only one of the habitat types found on Jamaica or Puerto Rico (the montane species *A. reconditus* from Jamaica) is not also found on both Hispaniola and Cuba. By contrast, many of the habitat specialists on Hispaniola (e.g. *Chamaelinorops barbouri*, *A. etheridgei*) and Cuba (e.g. *Chamaeleolis* species, *A. vermiculatus*) have no ecological counterpart on any of the other islands (note that *Chamaeleolis* and *Chamaelinorops* are phylogenetically part of the *Anolis* radiation; Hass *et al.* 1993).

These conclusions lead me to present the following hypothesis for the species–area relation within the Greater Antilles. First, a core set of six types of habitat specialists, termed ecomorphs (Williams 1972), is present on most or all of the Greater Antilles (the exceptions being the lack of grass anoles on Jamaica and trunk anoles on Jamaica and Puerto Rico). Within each of these islands, most or all of the ecomorph types are present at most localities and generally are more abundant than other types of habitat specialists (although twig anoles and crown-giants are often rarer than the other ecomorphs). Further, as already noted, some of the ecomorph types can be represented by many species on a single island. Second, other than ecomorph species, few other types of habitat specialist are represented by more than one species on an island. The only exceptions are three rock-dwelling members of the *monticola* series on Hispaniola (two sympatric), three bush-inhabiting species of the *argillaceus* series on Cuba (two probably sympatric), two species of the *lucius* group on Cuba (allopatric), and four species of *Chamaeleolis* on Cuba (only two of which can be found at any given locality).

Consequently, the increase in species number on large Greater Antillean islands reduces to two factors: first, lineages of the six common ecomorphs diversify by producing many allopatrically distributed species and a number of species capable of coexisting in sympatry. Second, many unique types of habitat specialists have evolved on the larger islands. The first factor may simply be a consequence of larger islands affording greater opportunities for allopatric speciation, as discussed above. Certainly, the existence of these allopatric species indicates that allopatric speciation occurs on these islands. In turn, this larger pool of reproductively isolated species enhances the possibility that some of these species will evolve ecological differences sufficient to permit sympatry.

The increased number of habitat types on the larger islands is less readily explained. Certainly, habitat availability would not seem to differ among the islands, all of which have wet and dry forests and high mountain ranges. One possible explanation is that the greater pool of species on larger islands enhances the possibility that one species will diverge sufficiently to utilize a distinctive habitat niche. This hypothesis makes the prediction that species utilizing unique habitats should have arisen within a lineage of a particular ecomorph type and should render such lineages paraphyletic. Although the phylogenetic affinities of many of these species are not clear-cut, the only evidence to date that supports this hypothesis is from the Jamaican *A. reconditus*, which may have evolved from within the Jamaican trunk-ground lineage (D. Irschick, personal communication). In contrast, most of the data seem to suggest that once a lineage has specialized to a particular habitat niche, it rarely evolves away from this specialization.

A third possibility is that the greater diversity of sympatric assemblages on larger islands forces lineages to specialize in ways not seen on small islands. Perhaps a hierarchy of habitat niches exists such that species evolve to occupy certain niches only after others have been occupied. This hierarchy, or deterministic pathway, might result either because specialization for some niches is evolutionarily more accessible than specialization for other niches, or because the adaptive peaks (*sensu* Simpson 1953) of some niches are higher than others. This hypothesis will prove difficult to test and does not accord with the observation that some unique habitat species occur in assemblages containing few other anole species (Williams 1983). Better phylogenetic information will be necessary to provide insight into how, and possibly why, these unique habitat species evolved.

7. CONCLUSIONS

The species–area relation among anoline lizards is more complicated than it appears on first inspection. Only by detailed examination of differences in island types and relations among taxa was it possible to discover the heterogeneity in the importance of different factors in determining species number on different islands. Broad scale studies involving many taxa are important for documenting general patterns and suggesting general hypotheses, but such studies must be complemented by more detailed studies of particular groups to fully understand patterns of species diversity (Williams 1969, 1983).

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